SIMOSTHENURUS NEWTONAE SP. NOV., A WIDESPREAD STHENURINE KANGAROO (DIPROTODONTIA: MACROPODIDAE) FROM THE PLEISTOCENE OF SOUTHERN AND EASTERN AUSTRALIA

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PRIDEAUX, G. J. 2000. *Simosthenurus newtonae* sp. nov., a widespread sthenurine kangaroo (Diprotodontia: Macropodidae) from the Pleistocene of southern and eastern Australia. *Records of the South Australian Museum* **33**(1): 1–15.

Simosthenurus newtonae sp. nov. is described from the Pleistocene of southern and eastern Australia. Its cranium is similar in size to *Simosthenurus occidentalis*, but is less brachycephalic and has a narrower, more elongate rostrum with a less inflated frontal region. The moderately high-crowned molars are distinctive among the species of *Simosthenurus*, because they bear very few to no fine enamel crenulations, and primary crests that bear strong contacts with cusp apices. In these respects, the molars resemble *Sthenurus andersoni* and *Hadronomas puckridgi*.

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Sthenurines were a diverse group of robust browsing kangaroos common throughout southern and eastern Australia in the Pleistocene. *Simosthenurus newtonae* sp. nov. represents the seventh new sthenurine described since 1992. Although uncommon in most assemblages, it is one of the more widely distributed sthenurines, occurring in 21 localities (Fig. 1). The description of this new species forms the subject of this paper. A review of the phylogenetic relationships, chronology, zoogeography and evolution of the sthenurine kangaroos is currently in preparation.

Materials And Methods

Specimens referable to *Simosthenurus newtonae* sp. nov. are housed in the vertebrate palaeontological collections of the following institutions: Australian Museum, Sydney (AM); South Australian Museum, Adelaide (SAM); Field Museum of Natural History, Chicago (FMNH); Flinders University of South Australia, Adelaide (FU); Museum of Victoria, Melbourne (NMV); Queensland Museum, Brisbane (QM); Queen Victoria Museum, Launceston (QVM); Western Australian Museum, Perth (WAM). Serial designation of the cheek dentition follows Flower (1867), Wilson and Hill (1897) and Luckett (1993), except that the third adult premolars are now recognised as the only second generation cheek teeth in marsupials (Cifelli *et al.* 1996; Luckett and Woolley 1996). Dental nomenclature follows Tedford and Woodburne (1987), Ride (1993) or is standard. Mensuration follows Tedford (1966) and Wells and Murray (1979). All measurements are in millimetres.

Systematics

Order DIPROTODONTIA Owen 1866

Superfamily MACROPODOIDEA Gray 1821

Family MACROPODIDAE Gray 1821

Subfamily STHENURINAE (Glauert 1926)

Genus ***Simosthenurus*** Tedford 1966

Simosthenurus newtonae sp. nov.
Sthenurus oreas DeVis (in part), 1895: 97.
Sthenurus atlas Glauert, 1912: 64.
Sthenurus andersoni Bartholomai (in part), 1963: 58, fig. 3.
Sthenurus sp. Lundelius, 1963: 77, fig. 2.
Sthenurus sp. cf. *S. gilli* Merrilees, 1965: 29–30.
Sthenurus andersoni Tedford (in part), 1966: 25.
Sthenurus sp. II Marcus, 1976: 71, 74, fig. 27c–d.
Simosthenurus sp. II Pledge, 1980: 137, table 3.
Sthenurus sp. Williams, 1980: 107, site 30.
Sthenurus sp. cf. *S. atlas* Williams, 1980: 107, site 37.

FIGURE 1. Localities yielding remains of *Simosthenurus newtonae* sp. nov. (black squares): 1, Tight Entrance Cave; 2, Balladonia; 3, Madura Cave; 4, Lindsay Hall Cave; 5, Curramulka Quarry; 6, Black Rock Gravel Pit; 7, Baldina Creek; 8, Comaum Forest Cave; 9, Haystall Cave; 10, Henschke's Fossil Cave; 11, SOS Cave; 12, Victoria Fossil Cave; 13, Goulden's Hole; 14, Green Waterhole Cave (*Type locality*); 15, Kilsby's Hole; 16, McEachern's Cave; 17, Scotchtown Cave; 18, Teapot Creek; 19, Kandos; 20, Wellington Caves; 21, Darling Downs. Triangles denote localities yielding *Simosthenurus occidentalis.*

Sthenurus sp. Lundelius & Turnbull, 1989: 2, 4, fig. 1a.
Simosthenurus sp. nov. Prideaux & Wells, 1994: 227.
Sthenurus 'P17250' McNamara, 1994: 111, 115.
Sthenurus 'P17250' Prideaux & Wells, 1997: 191, 194.

Holotype

SAM P17249–P17250, partial adult cranium, and fused left and right dentaries (Figs. 2, 3).

Type Locality

Green Waterhole Cave, a submerged cave near Tantanoola, southeastern South Australia. Faunal composition suggests a late Pleistocene age (Pledge 1980; Newton 1988).

Paratypes

FU 0227, near complete adult cranium; FU 0252, juvenile cranium devoid of occipital region; SAM P20255–P16632–P16633, partial adult cranium, incomplete left and right dentaries; SAM

P28969, near complete, but crushed adult cranium; FU 0179, right dentary. All paratypes are from the Fossil Chamber in Victoria Fossil Cave, Naracoorte, southeastern South Australia. This locality is considered to be late Pleistocene, but is probably older than 212 000 years (Wells *et al.* 1984; Ayliffe *et al.* 1998).

Referred Specimens

Victoria Fossil Cave, Naracoorte, SA: FU 0205, partial right juvenile dentary; FU 0226, right M_3; FU 0259, partial left juvenile dentary; FU 0293, partial left adult dentary; FU 0887, partial left juvenile maxilla; FU 1084, partial left juvenile maxilla; SAM P16550, partial juvenile cranium; SAM P20243, partial left adult maxilla; SAM P27631, left I_1, M_{1-2}; SAM P28149, partial left adult dentary; SAM P28478, right P_3; SAM P28479, right M_1, M_3; SAM P28518, left I_1; SAM P28671, left juvenile dentary; SAM P28996, left juvenile dentary; SAM P32533, left M_3; SAM P32541, left I_1; SAM P32542, left I_1, M_3; SAM P32545, partial right juvenile dentary.

Haystall Cave, Naracoorte, SA: SAM P36624, right dP_2.

Henschke's Fossil Cave, Naracoorte, SA: SAM P17837, partial left juvenile maxilla, right dP^2, right M^1; SAM P18554, right M^1 metaloph; SAM P34807, right P^3; SAM P34808, left P^3; SAM P34809, right P^3; SAM P34810, right P_3; SAM P34811, left P^3; SAM P38788, dP_{2-3}, P_3, M_{1-2}, right P_3, M_1; SAM P38789, left and right M^4; SAM P38790, left P_3; SAM P38791, right M_4; SAM P38792, left P^3; and SAM P unregistered, several loose teeth.

SOS Cave, Naracoorte, SA: SAM P33476, partial right adult maxilla.

Comaum Forest Cave, near Penola, SA: SAM P31967, fused left and right premaxillae and maxillae.

Goulden's Hole, near Mount Schank, SA: SAM P36620, right P^3; SAM P36621, left P_3; SAM

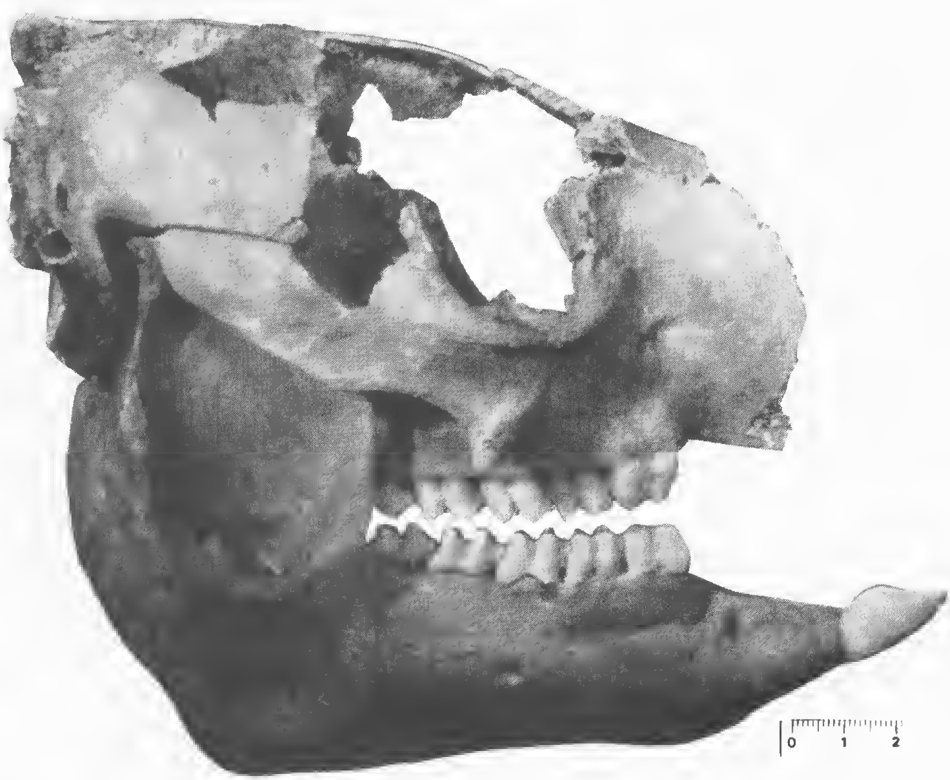

FIGURE 2. Right lateral view of partial cranium and dentaries of *Simosthenurus newtonae* sp. nov. holotype, SAM P17249 / P17250. Small gradations on scale bar are millimetres.

P36622, left M^1; SAM P38780, left M^4; SAM P38781, left M_4.

Kilsby's Hole, Mount Gambier, SA: SAM P38782, left P^3, SAM P38783, right lower molar, SAM P38784, left upper molar, SAM P38785, right dP_2.

Black Rock Gravel Pit, near Orroroo, SA: SAM P23166, left and right adult dentaries.

Baldina Creek, Burra, SA: SAM P21035, partial juvenile dentary.

Curramulka Quarry, Yorke Peninsula, SA: SAM P38786, right P^3, SAM P38787, right P_3.

McEachern's Cave, near Nelson, VIC: SAM P17319, partial right adult dentary; NMV P198434–P198438–P198440, left and right adult maxillae; NMV P198435–P198436, left and right adult maxilla; NMV P198439, partial left adult dentary; NMV P198449, partial left adult maxilla; NMV P198450, right P^3 in maxilla fragment.

Teapot Creek, Monaro Region, NSW: AM F unregistered, partial right adult dentary.

Wellington Caves, NSW: AM F18872, left P^3.

Kandos, NSW: AM F73721, partial left adult dentary.

Darling Downs, southeastern QLD: QM F2978, partial right adult maxilla.

Scotchtown Cave, near Smithton, TAS: QVM:1992:GFV:232, right M_3; QVM:1992:GFV:238, right M^3; QVM:1992:GFV:242, right M^1.

Madura Cave, Madura, WA: FMNH PM4356, right P_3.

Lindsay Hall Cave, near Madura, WA: WAM 92.12.3, right M^1; WAM 92.12.10, right M^3; WAM 00.1.1, partial right juvenile maxilla.

Balladonia Soak, near Balladonia, WA: WAM 63.11.2–63.11.3, right adult dentary.

Tight Entrance Cave, southwestern WA: WAM

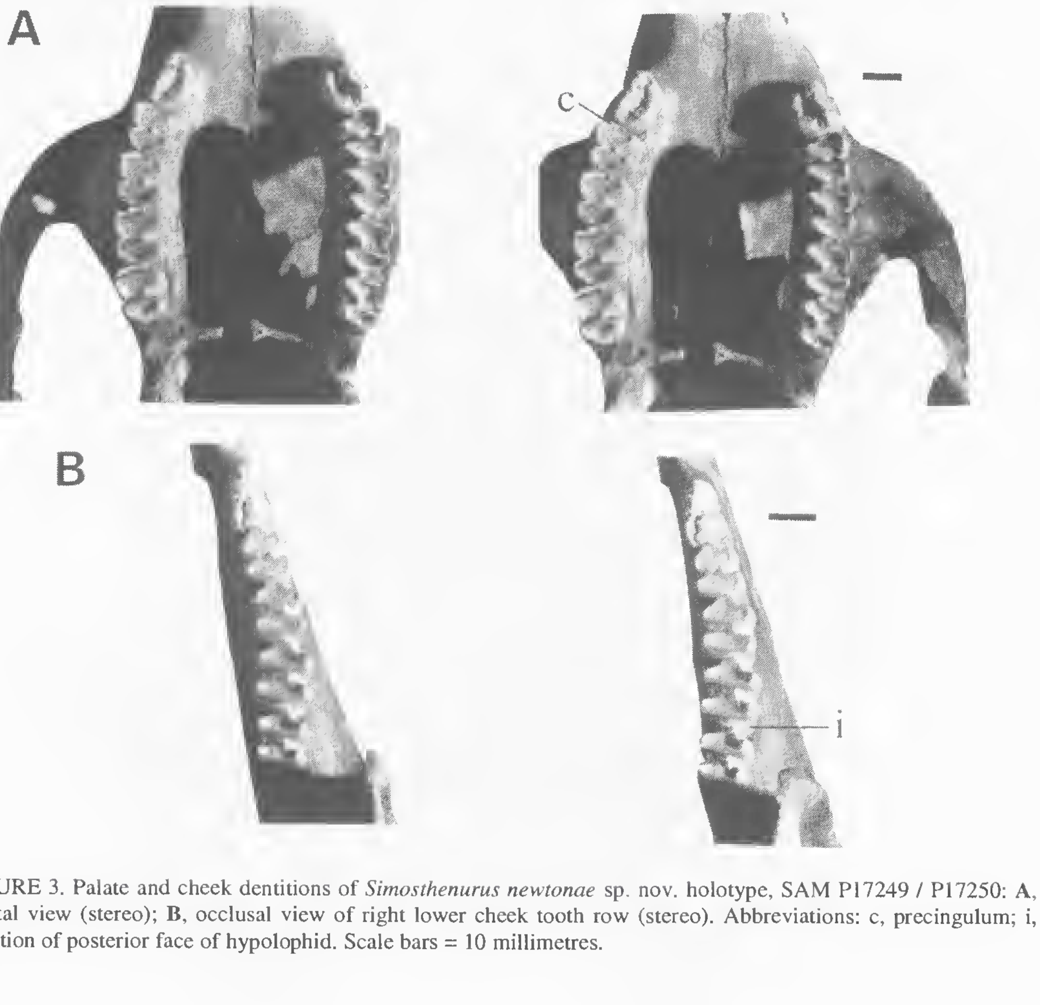

FIGURE 3. Palate and cheek dentitions of *Simosthenurus newtonae* sp. nov. holotype, SAM P17249 / P17250: **A**, palatal view (stereo); **B**, occlusal view of right lower cheek tooth row (stereo). Abbreviations: c, precingulum; i, inflation of posterior face of hypolophid. Scale bars = 10 millimetres.

97.5.312–97.5.314–97.5.314–99.11.142, left adult dentary.

Species Diagnosis

Cranium similar in size to *Simosthenurus brownei* Merrilees 1967 and *Si. occidentalis* Glauert 1910, but less brachycephalic, with narrower, more elongate rostrum, longer diastema and less inflated frontal region. Masseteric process short, narrowing distally and twisted posteriorly. P^3 short for width, crown inflated anterobuccally and thus only slightly wider posteriorly than anteriorly. Upper and lower molars relatively high-crowned with very few to no fine enamel crenulations. Crests on molars very well-developed, generally maintaining strong contact with cusp apices. Precingulum abruptly terminated at position of preprotocrista. Pterygoid fossa narrow and dorsoventrally deep. Lower molars bear pronounced anterior turn of lophid ends and strongly inflated posterior face of hypolophid.

Etymology

The new species is named after Cate A. Newton who studied the fossil fauna of Green Waterhole Cave and first recognised the morphological uniqueness of the holotype.

Description

Cranium (Figs 2–5; Table 1).

Premaxilla rather slender in lateral view, but flaring dorsally for extended contact with nasal. Incisor-bearing portion of premaxilla rather shallow and elongate (Fig. 5). Diastema moderately elongate, maxilla-premaxilla suture elongate and zigzagged. Cranial diastema deflected anteroventrally relative to cheek tooth row. Incisive foramina long with anterior border opposite or just posterior to posterior extremity of I^3 alveolus. Rostrum narrow, deep and elongate. Anteorbital/buccinator fossae on maxilla very shallow, resulting in reduced mesial curvature of diastema ridge, and rather flat-sided maxilla anteroventral to centre of orbit. Nasals long, broad posteriorly, narrowing anteriorly. One to three infraorbital foramina anterior to ventral border of orbit. Masseteric process short, moderately wide, flaring slightly towards distal end, twisted posteriorly under anterior portion of jugal (Figs 2–5). Process consists primarily of maxilla with only modest jugal contribution. Frontal region rather elongate in dorsal view, only moderately inflated laterally (Fig. 4A). Palatine vacuities extend anteriorly to opposite M^1 precingulum. Postpalatine bars form a thin bridge across palate opposite or posterior to M^4 metaloph (Fig. 3A).

Basicranial plane markedly elevated above palatal plane. Cranial pterygoid fossa wide and deep. Basioccipital slightly flexed posterodorsally relative to basisphenoid, and bears well-developed medial keel. Zygomatic arch deep, with a very wide ectoglenoid process at posterior extremity of jugal. Postglenoid process and glenoid fossa very large. Temporal crests not fully convergent on sagittal suture and only moderately developed. Occipital region broad, but not especially deep, and oriented at 90° relative to dorsal surface of neurocranium. Vertical medial occipital crest

TABLE 1. Mean dimensions of the adult cranium and dentary of *Simosthenurus newtonae* sp. nov. compared with the dimensions of the holotype (SAM P17249–P17250) and mean dimensions of *Simosthenurus occidentalis* and *Sthenurus andersoni*. Standard deviation is given in parentheses; sample size in brackets.

Dimension	*Simosthenurus newtonae*	Holo-type	*Simosthenurus occidentalis*	*Sthenurus andersoni*
Condylobasal Length	216 (3.0) [n=3]	–	198 (4.9) [n=4]	221 (8.5) [n=2]
Diastema Length	40.3 (1.04) [n=4]	–	31.8 (1.42) [n=4]	47.2 (4.38) [n=2]
% Diastema Length: Palatal Length	30.5 (0.85) [n=3]	–	25.2 (0.01) [n=4]	36.0 (2.83) [n=2]
Palatal Length	132 (1.2) [n=3]	–	126 (4.1) [n=4]	132 (2.1) [n=2]
Palatal Width between M^1 Protolophs	37.2 (2.27) [n=5]	39.0	35.0 (0.46) [n=3]	38.8 (0.92) [n=2]
Palatal Width between M^4 Protolophs	39.2 (4.05) [n=3]	43.1	41.2 (0.53) [n=3]	42.1 (0.14) [n=2]
Max. Width across Zygomatic Arches	132 (5.6) [n=4]	136	143 (1.53) [n=3]	114 (2.1) [n=2]
Maximum Width across Frontals	77.5 (3.05) [n=4]	82.0	91.8 (3.22) [n=4]	63.4 (1.98) [n=2]
Width across Paroccipital Processes	76.3 (5.12) [n=4]	82.0	67.7 (2.67) [n=3]	62.7 (3.25) [n=2]
Dentary Depth	34.8 (3.35) [n=5]	39.3	37.6 (1.70) [n=13]	28.4 (1.82) [n=10]
Dentary Width	20.5 (1.20) [n=5]	20.6	23.4 (2.03) [n=13]	17.2 (2.04) [n=10]
Dentary Depth / Width	1.70 (0.13) [n=5]	1.91	1.62 (0.14) [n=13]	1.65 (0.13) [n=10]

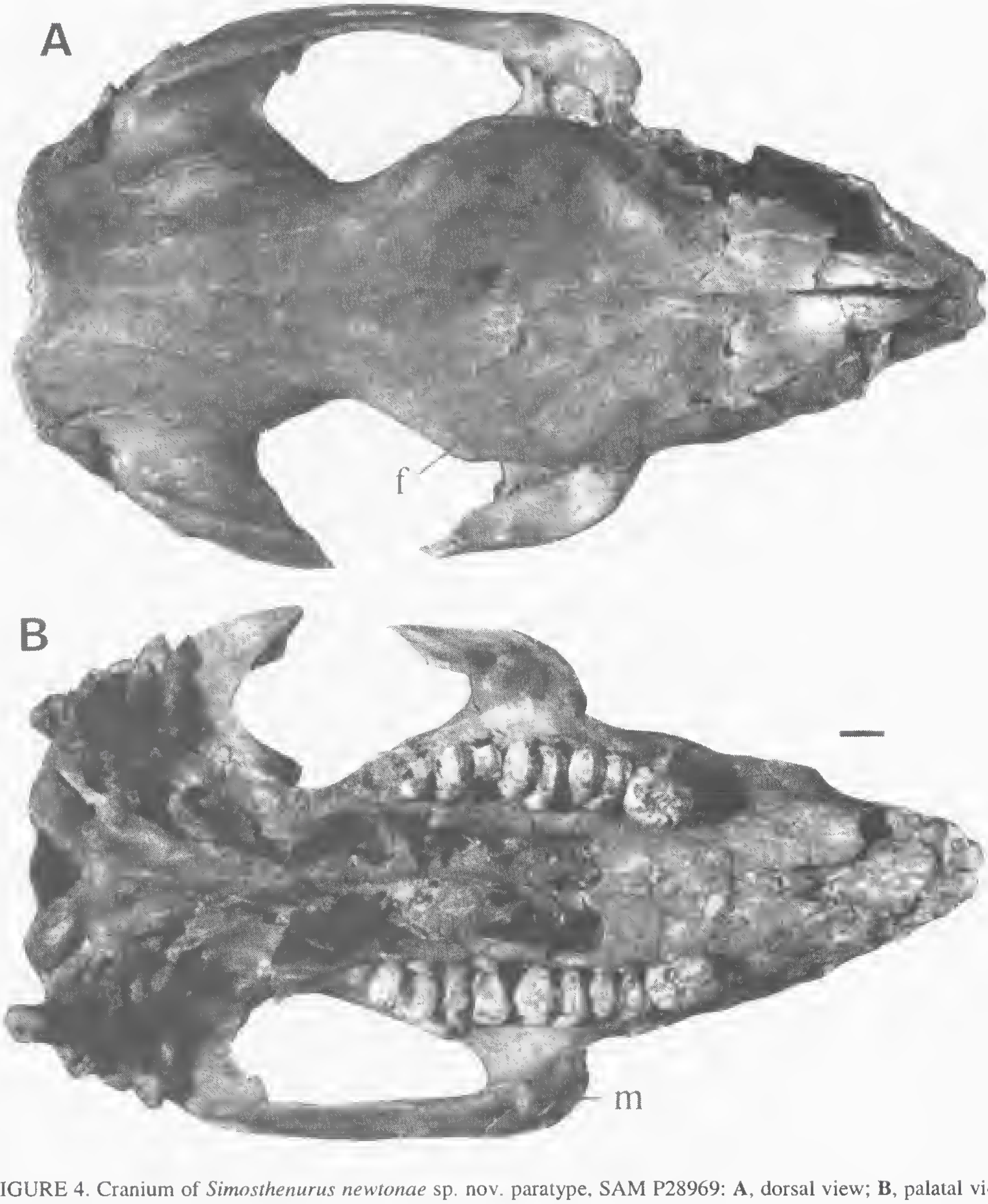

FIGURE 4. Cranium of *Simosthenurus newtonae* sp. nov. paratype, SAM P28969: **A**, dorsal view; **B**, palatal view. Abbreviations: f, frontal; m, masseteric process. Scale bar = 10 millimetres.

slight to well-developed, and leads ventrally to wide foramen magnum bordered by moderately large occipital condyles. Paroccipital processes deflected posteroventrally. Nuchal crests strongly-developed and extended posteriorly (Fig. 4A).

Upper Dentition (Figs 2–5; Table 2).

I^1 quite low in crown height and rather rounded in cross-section (Figs 4–5). Vertical occlusal facet faces posteriorly. Strongly curved anterior surface of crown extends forward well beyond anterior extremity of premaxilla. I^2 round in cross-section, one-third size of I^1. I^3 unknown, but alveolus suggests elongate crown.

Second upper deciduous premolar (dP^2) reminiscent of P^3 in general morphology, but

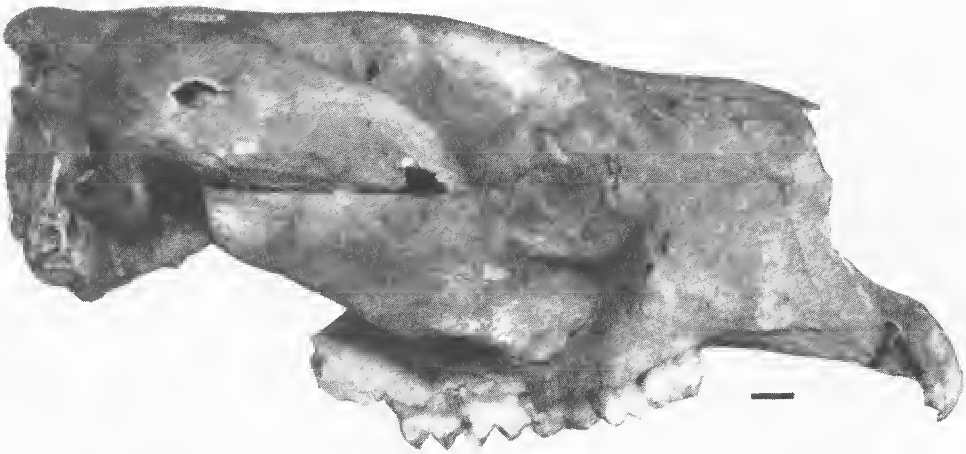

FIGURE 5. Right lateral view of partial cranium of *Simosthenurus newtonae* sp. nov. paratype, SAM P20255. Scale bar = 10 millimetres.

much shorter relative to width. Outline of tooth very rounded, especially on lingual side. Main crest straight and aligned with antero-posterior plane of tooth, lingual crest very curved and much lower in height than main crest. Anterior basin absent. Posterior basin well-developed, half size of longitudinal basin and separated by marked transverse ridge. Third upper deciduous premolar (dP^3) completely molariform, narrower across protoloph than metaloph and smaller than molars. Small precingulum restricted to buccal two-thirds of protoloph face, terminating at position of preprotocrista. Unworn crest of protoloph very convex anteriorly with very thick, united postparacrista and premetacrista. Remaining aspects very similar to molars, except for fine postlink and crest centred on posterior face of protoloph. P^3 usually short for width, only slightly wider posteriorly than anteriorly (Figs 3–5; Table 2). Outline rounded, with anterobuccal aspect strongly inflated and lingual side convex. Posterobuccal accessory cusp absent, poorly differentiated or slight, very occasionally with small, poorly differentiated cuspule anterior to it. Lingual crest lower and usually more curved than main crest. Anterior basin small and not well differentiated. Longitudinal basin short, of modest width and depth, and occupied by fine to coarse transverse ridgelets. Posterior basin well-developed, and separated from longitudinal basin by strong transverse ridge formed by two strong ridgelets united at tooth midline, or by buccally curved end of lingual crest.

Upper cheek tooth row moderately curved buccally, with P^3 turned in slightly relative to molars (Figs 3A, 4B). Upper molars sized $M^1<M^2<M^3>M^4$ (Figs 2–5; Table 2). Metaloph narrower relative to protoloph on M^4 than on M^{1-3}. Lophs moderately high-crowned, with unworn crests slightly convex anteriorly. Loph faces bear few very fine or no enamel crenulations. Preparacrista strongly developed, and maintains strong, direct contact with paracone apex. Precingulum smoothly confluent with preparacrista and terminates at tiny remnant of preprotocrista, after extending across two-thirds of anterior face of protoloph (Fig. 3A). Prominent postprotocrista ascends posterobuccally into interloph valley, but only extends onto base of metaloph face as very short, fine crest. Well-developed postparacrista and moderately developed premetacrista curve in lingually, their union forming a distinct notch. Posterior face of metaloph dominated by well-developed postmetaconulecrista, which curves buccally across approximately three-quarters of posterior face of metaloph to meet similarly-developed postmetacrista. Tiny cuspule positioned at union of postmetaconulecrista and postmetacrista most prominent on M^3, and probably represents stylar cusp E. Posterior face of metaloph markedly inflated above postmetaconulecrista, especially more buccally.

<u>Dentary</u> (Figs 2, 3, 6; Table 1).

Ramus deep for width, especially posteriorly due to large digastric eminence (Figs 2,6), which curves in mesially along ventral border. Digastric

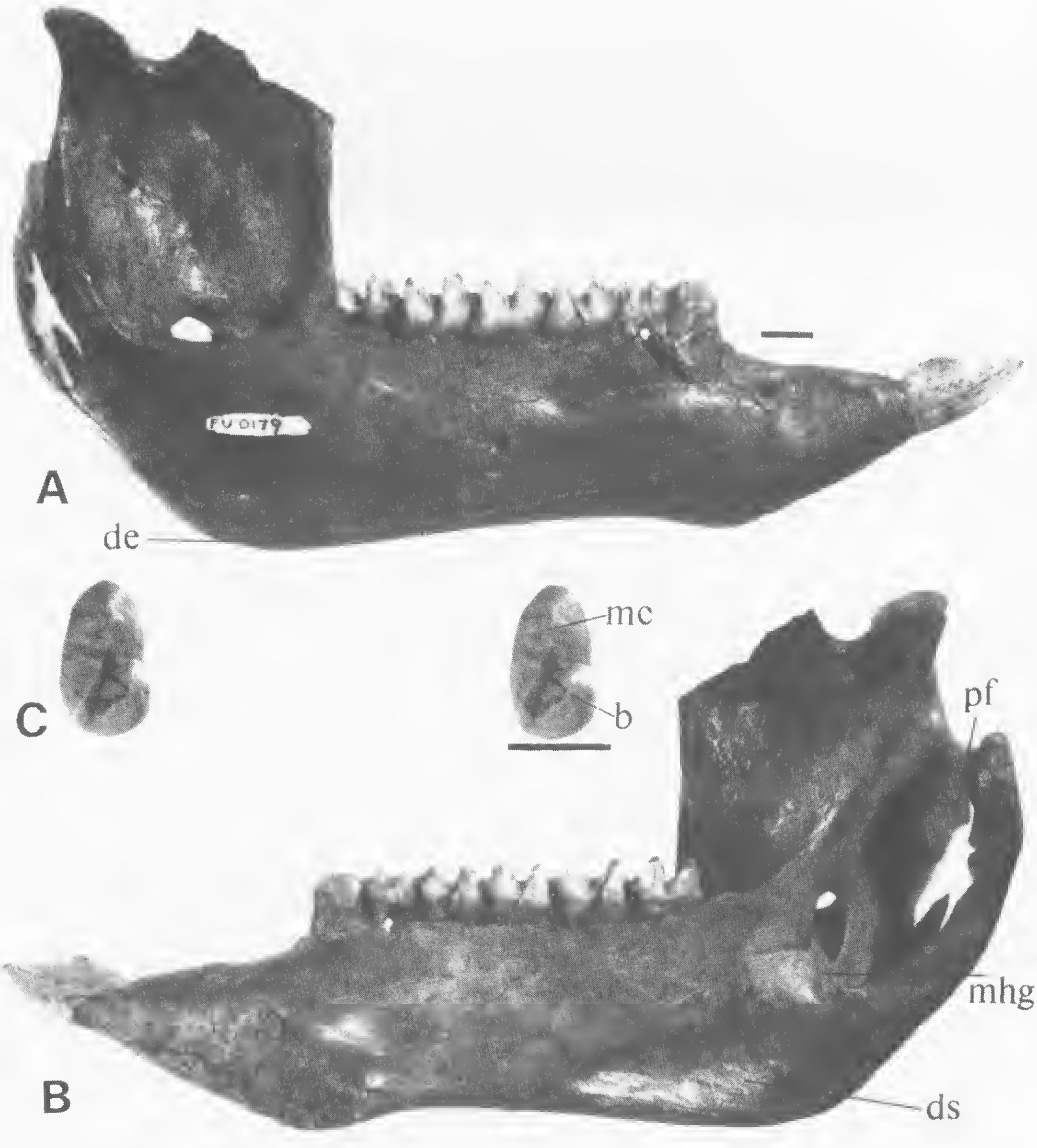

FIGURE 6. Right dentary of *Simosthenurus newtonae* sp. nov. paratype, FU 0179: **A**, lateral view; **B**, mesial view; **C**, occlusal view of excavated right P_3 (stereo). Abbreviations: b, buccal crest; de, digastric eminence; ds, digastric sulcus; mc, main crest; mhg, mylohyoid groove; pf, pterygoid fossa. Scale bars = 10 millimetres.

sulcus large and extends anteriorly to beneath M_2 hypolophid or M_3 protolophid (Fig. 6B). Dentary decreases in depth anteriorly, with diastema somewhat procumbent relative to cheek tooth row (Figs 2, 6). Symphysis rather slender and procumbent, with dorsal border parallel with alveolar margin of cheek tooth row. Posterior portion of symphysis underlies small genial pit, and only extends to beneath posterior root of P_3. Median dorsal groove deep and narrow. Anterior mental foramen located just anteroventral of buccinator sulcus. Buccinator sulcus shallow anteriorly, but gradually deepens posteriorly, terminating beneath M_1 hypolophid. Posterior mental foramen mid-depth on ramus beneath M_2 hypolophid.

Ascending ramus rather short in lateral profile with anterior root located adjacent to M_4 hypolophid (Figs 2, 6). Anterior root forms buccal aspect of wide, deep postalveolar fossa. Masseteric foramen large and elliptical, leading into deep vertical masseteric canal which does not extend into body of ramus. Inferior mandibular foramen usually fairly large, with dorsal border at level of alveolar margin of cheek tooth row. Pterygoid fossa high and narrow, bearing pronounced upward projection of angular process (Figs 2, 6). Adjacent to ventral border of inferior mandibular foramen and at anterior extremity of pterygoid fossa, two sharp processes overhang mylohyoid groove; a posteroventrally-oriented process (cf. lingula in humans) and an anterodorsally-oriented process extending from anterior end of mesial border of pterygoid fossa (Fig. 6B). Mandibular condyle large.

Lower Dentition (Figs 2, 6; Table 2).

I_1 large, robust, elongate (Figs 2, 6). Occlusal surface slightly higher than, but oriented close to parallel with diastema. Level of I_1 occlusal surface well below level of cheek tooth occlusal surfaces. Second lower deciduous premolar (dP_2) similar in overall morphology to P_3, but shorter relative to width. Main crest runs obliquely across tooth from posterolingual corner to central position anteriorly. Short buccal crest trends buccally from posterior extremity of main crest, then curves anteriorly to run parallel to posterior part of main crest for short distance. Third lower deciduous premolar (dP_3) completely molariform, with protolophid slightly narrower than hypolophid and tapered markedly toward relatively narrow unworn crest. Small paraconid positioned at anterior extreme of trigonid, lingual to end of paracristid. Premetacristid runs posteriorly from paraconid, terminating midway up metaconid anterior face. Thick ?parametacristid descends smoothly from metaconid apex terminating in middle of trigonid basin. ?Preprotostylocristid runs anteriorly from topographic protoconid apex to point where paracristid turns lingually. Cristid obliqua strongly-developed, continuous with buccal extremity of hypolophid, meets protolophid slightly posterolingual and ventral to protoconid. Preentoconid low, curves from entoconid apex into interlophid valley to near midline of tooth. Very slight posterobuccally-accentuated inflation present on posterior face of hypolophid. Lophid faces lack enamel crenulations.

P_3 small and moderately short relative to molars, usually similar to or slightly shorter than M_3 in length (Figs 2, 3, 6; Table 2). Posterobuccal aspect of tooth inflated and bearing short, thick buccal crest separated from posterior end of main crest by very shallow, narrow median valley in holotype (Fig. 3B). In paratypes and referred specimens, inflation of posterobuccal corner less marked; buccal crest usually slightly longer and bears a thin, crescentic buccal crest separated from main crest by small and shallow median valley (Fig. 6C). Cuspules of main crest poorly differentiated posteriorly, but three usually distinguishable anteriorly. Very few to no ridgelets traverse median valley.

Lower cheek tooth row shows slight to moderate buccal curvature, with main crest of P_3 oriented slightly anterobuccally relative to molars (Fig. 3B). Moderately high-crowned lower molars sized $M_1<M_2<M_3>M_4$ (Figs 2, 3, 6, Table 2). Lophid faces often lack enamel crenulations, but a few very fine crenulations may be present on anterior faces. Anterior turn of lophid ends very pronounced (Fig. 3B). Paracristid and cristid obliqua well-developed, with former maintaining contact with topographic protoconid apex, and latter contacting or very close to hypoconid apex (Fig. 3B). Precingulid/trigonid shelf narrow and moderately short. Transverse (anterior) portion of paracristid broadly U-shaped in unworn teeth, curving out to anterior extremity of tooth, above precingulid, then posteriorly, usually uniting with fine, low premetacristid. ?Parametacristid either slight or absent. Cristid obliqua on minimally worn teeth divided into anterior and posterior components, although moderate wear produces one continuous crest. Lower posterior component curves smoothly anteriorly from hypoconid apex and terminates on buccal side of anterior component, located closer to midline of tooth and oriented less obliquely. Anterior component of cristid obliqua extremely slight anterior to interlophid valley, fining and terminating midway up posterior protolophid face. Preentoconid low and very slight. Shelf-like postcingulid absent, but buccal two-thirds of posterior aspect strongly inflated more ventrally, and overlapped by trigonid of succeeding molar (Figs 3B, 6A).

Intraspecific Variation

Cranium

There is very little variation in the general size and morphology of known adult crania that cannot be ascribed to differential preservation. The only noteworthy variation is a slight difference in

TABLE 2. Cheek tooth dimensions of *Simosthenurus newtonae* sp. nov., showing mean and standard deviation (in parentheses), dimensions of the holotype (SAM P17249–P17250), and the Wellington Caves and Kandos specimens (AM F18872, AM F73721).

Tooth	**Length**	**Anterior Width**	**Posterior Width**	**Anterior Height**	**Posterior Height**	**Sample Size**
UPPER DENTITION						
dP^2	10.3 (0.91)	7.7 (0.51)	9.6 (0.97)	7.1 (0.47)	7.8 (0.81)	3
dP^3	11.5 (0.20)	9.8 (0.66)	10.9 (0.42)	6.2 (0.85)	7.0 (1.15)	3
P^3						
Mean	16.6 (0.72)	10.5 (0.82)	12.3 (0.52)	10.4 (0.61)	10.1 (0.86)	15
Holotype	16.9	10.6	12.9	11.0	10.8	
AM F18872	18.3	10.0	13.4	10.3	9.8	
M^1						
Mean	13.2 (0.32)	12.9 (0.50)	12.6 (0.38)	7.7 (0.79)	7.9 (0.71)	11
Holotype	13.2	13.1	12.8	8.3	8.0	
M^2						
Mean	14.5 (0.60)	13.9 (0.82)	13.0 (0.65)	8.2 (0.71)	8.4 (0.71)	12
Holotype	14.7	13.7	13.0	9.0	8.7	
M^3						
Mean	15.0 (0.59)	13.7 (0.53)	12.9 (0.63)	7.9 (0.48)	7.9 (0.37)	12
Holotype	15.0	13.8	13.3	8.3	8.3	
M^4						
Mean	14.1 (0.67)	12.9 (0.36)	11.1 (0.42)	6.6 (0.55)	6.2 (0.52)	8
Holotype	14.8	13.0	11.5	7.5	6.6	
LOWER DENTITION						
dP_2	9.5 (0.68)	6.1 (0.49)	8.1 (0.31)	7.9 (0.95)	7.1 (0.83)	6
dP_3	10.4 (0.21)	8.3 (0.57)	8.8 (0.53)	7.1 (0.89)	7.2 (0.90)	6
P_3						
Mean	15.3 (0.74)	7.6 (0.43)	9.3 (0.33)	10.1 (0.79)	9.4 (1.16)	16
Holotype	15.3	7.7	9.7	10.0	10.1	
AM F73721	17.5	8.4	9.9	–	–	
M_1						
Mean	13.1 (0.67)	10.2 (0.37)	10.5 (0.35)	9.2 (0.98)	9.7 (1.47)	14
Holotype	13.1	10.1	10.7	9.1	9.7	
AM F73721	14.3	11.4	11.7	–	–	
M_2						
Mean	15.2 (0.61)	11.3 (0.38)	11.6 (0.34)	10.0 (1.38)	10.4 (1.35)	12
Holotype	15.7	11.5	11.7	9.2	9.6	
AM F73721	16.0	12.5	13.0	–	–	
M_3						
Mean	16.3 (0.45)	12.1 (0.29)	12.3 (0.42)	9.5 (1.43)	9.4 (1.25)	11
Holotype	16.6	12.1	12.4	9.5	9.5	
AM F73721	17.3	13.5	13.8	10.1	11.7	
M_4						
Mean	14.6 (0.79)	11.5 (0.28)	10.4 (0.44)	8.4 (0.74)	7.3 (0.55)	8
Holotype	15.8	11.3	10.7	8.6	7.3	
AM F73721	17.0	13.0	12.2	10.8	10.3	

zygomatic arch depth, with SAM P28969 shallower than SAM P17249, SAM P20255 and FU 0227.

The juvenile cranium, FU 0252 (dP^{2-3}, M^{1-2} erupted), clearly differs from the adult crania in proportion. The rostrum is relatively longer, the ventral orbital border of the jugal is less laterally expanded, the frontal region is less inflated, the temporal crests are less convergent upon one another, and the width across the zygomatic arches is comparatively less.

Upper Dentition

No appreciable variation is visible in I^1 size or morphology between the four specimens preserving that tooth. These same specimens also preserve I^2 but, in contrast to I^1, I^2 of SAM P20255 is slightly smaller in cross-sectional area than in the other specimens, even taking into consideration its greater degree of wear. Minimal size or morphological variation has been observed for dP^2, aside from the presence of an incipient posterobuccal accessory cusp in SAM P16550, a low, slight posterobuccal cingulum in FU 1084, and the complete absence of any such feature in FU 0252 and FU 1084. The longitudinal basin is slightly larger in FU 0252 than FU 1084, but SAM P16550 is too worn to determine. No notable size or morphological variation is visible in dP^3. Upper molar variation is also very limited, with the slightest fine enamel crenulations visible on the unworn molars of some specimens.

Marked variation exists in both size and morphology between the P^3 of the holotype, paratypes and referred specimens. Size differences are present in absolute length and width, crown height, and width relative to length, although no geographically-correlated size variation is evident. Morphological variation is displayed in: a) degree of posterobuccal accessory cusp development (ranging from clearly defined with small anterior cuspule, to poorly differentiated, to completely absent); b) degree of curvature of lingual crest and degree to which both crests are divided into cuspules; c) nature of coarse ridgelet separating posterior and longitudinal basins (composed of continuation of lingual crest or two transverse ridgelets); d) general inflation or roundness of tooth outline.

It is worth singling out a rather large, unworn P^3 from Wellington Caves (AM F18872) for special consideration, because it is much wider posteriorly than anteriorly. Although this conflicts with one of the defining characteristics of *Si. newtonae*, all other features of the tooth fit within the recognised *Si. newtonae* morphospace. These features include the inflation of the anterobuccal corner, shape of the lingual crest relative to the main crest, presence of one small cuspule immediately anterior to a poorly differentiated posterobuccal accessory cusp, and buccal curvature of the posterior end of the lingual crest, such that it partially separates the longitudinal and posterior basins. For these reasons, and because *Si. newtonae* is known from a dentary with rather large molars from nearby Kandos (AM F73721), I am confident that the Wellington Caves specimen is *Si. newtonae*.

Dentary

Few morphological differences are visible between the adult dentary specimens apart from slight variation in the posterior extent of the symphysis (beneath the anterior and posterior roots of P_3), and degree of development of the digastric eminence and sulcus. As a consequence of the latter variable feature, dentary depth varies slightly between specimens (e.g., compare the holotype dimensions with mean dimensions in Table 2). Variation is also present in the size of the inferior mandibular foramen and development of the processes overhanging the mylohyoid groove. Relatively, the holotype has the deepest dentary, largest inferior mandibular foramen and largest mylohyoid associated processes. Disregarding overall size differences, comparison of adult and juvenile specimens reveals a trend with age for increased dentary depth relative to width, and development of the digastric eminence and sulcus.

Lower Dentition.

No significant variation is visible in I_1 and dP_3. Similarly, there is little variation in dP_2, with only a slight difference between specimens in overall size, relative length of the buccal crest, and the variable presence of a ridgelet linking the anterior end of the buccal crest to the second cuspule of the main crest. While some size variation is evident in P_3, the considerable degree of morphological variation mirrors that observed in the P^3. Variation is displayed in: a) general tooth outline (rounded and gently narrowing anteriorly with minimal differentiation into anterior and posterior portions, posterobuccal corner inflated with much of buccal side and lingual side near parallel); b) shape of main crest (longitudinally straight, slightly sinusoidal); c) degree to which main crest cuspules are differentiated; d) relative length and shape of buccal crest (very short and thick, short and crescentic); e) low, fine ridgelet connecting buccal crest to second cuspule of main crest (absent, present); f) width of median valley and degree of development of contained ridgelets. The P_3 also varies slightly in the degree to which its longitudinal axis is deflected anterobuccally relative to the curvature of the molar row. The minimal variation noted for the upper molars also holds for lower molars.

The Kandos dentary (AM F73721) varies slightly from typical *Si. newtonae*, because its P_3 and molars are around 10% larger. This is noteworthy in view of the marked similarity in dental size between specimens of *Si. newtonae* from across its wide range, which includes western and Tasmanian representatives. Although the dentition is considerably worn, no morphological differences are evident between the cheek teeth of AM F73721 and similarly worn specimens of *Si. newtonae*. While it is important to note that the digastric region, ascending ramus and anterior portion of the ramus are missing in AM F73721, the dentary of this specimen only differs from other individuals of *Si. newtonae* by possessing a buccinator sulcus that is slightly deeper anteriorly. In view of the marked variation in size observed within other *Simosthenurus* species (Prideaux 1999), I have very little hesitation in referring this specimen to *Si. newtonae*.

Comparison with other taxa

Cranium.

The cranium of *Simosthenurus newtonae* is more dolichocephalic than that of any other *Simosthenurus* species. In relative skull length it is intermediate between the other *Simosthenurus* species and *Sthenurus* Owen 1874, resembling *Hadronomas puckridgi* Woodburne 1967 in this regard. Among the species of *Simosthenurus*, the *Si. newtonae* cranium is most similar to *Si. occidentalis*, but it differs by having a more elongate rostrum and diastema, and a less posterodorsally-flexed basioccipital region. Despite the otherwise similar occipital and basicranial proportions of the two species, the direct effect of these differences is that the portion of the cranium posterior to the end of the maxilla is longer in *Si. newtonae* than it is in *Si. occidentalis*. Inflation of the frontal region and development of the supraorbital crests are less pronounced in *Si. newtonae* than in *Si. occidentalis* and *Si. brownei*, but greater than in *Si. gilli* Merrilees 1965 and *Si. baileyi* Prideaux and Wells 1998. The masseteric process is shorter and much narrower than *Si. occidentalis*, and is closest in morphology to *Si. maddocki* Wells and Murray 1979, but more twisted posteriorly. Moderate development of the temporal crests is similar to *Si. baileyi*. The shallow anteorbital/buccinator fossae and reduced mesial curvature of the diastema border resemble *Si. baileyi* as well as *Si. gilli*, but both of these species have much shorter rostra.

Upper Dentition.

The general shape of the *Si. newtonae* I^1 is typical of most *Simosthenurus* species, but the tooth is quite low-crowned, akin to that of *Si. brownei*. Although the elongate I^3 alveolus probably indicates a relatively elongate crown, I have observed no I^3 which may be confidently ascribed to *Si. newtonae*. The dP^2 of *Si. newtonae* is smaller than in southeastern *Si. brownei* and *Si. occidentalis*, but larger than in *Si. maddocki* and *Sthenurus andersoni* Marcus 1962. Morphologically, the tooth recalls *Si. brownei* and *Si. baileyi*, but it is less inflated posteriorly. Although quite variable in form, the P^3 of most *Si. newtonae* individuals is quite dissimilar to the other *Simosthenurus* species. This is especially so because, relative to its length, the tooth is usually quite wide anteriorly as well as posteriorly. The manner in which the posterior end of the lingual crest curves buccally to partially or wholly separate the longitudinal and posterior basins is only seen elsewhere in *S. andersoni*, as well as a P^3 fragment from the early Pliocene Bow Local Fauna of central eastern New South Wales (see Fig. 1A in Flannery and Archer 1984). Marked inflation of the anterobuccal corner of P^3 is only seen in rare individuals of other *Simosthenurus* species.

The upper molariform teeth of *Si. newtonae* are unique among *Simosthenurus*, and cannot readily be confused with any other species. They are similar to *Si. baileyi* in size, but are easily distinguished by being higher-crowned, lacking any noteworthy enamel crenulations, and having the primary crests strongly connected to cusp apices. The smaller *Si. gilli* and *Si. maddocki* upper molars bear some resemblance to *Si. newtonae* in this latter feature, as well as the curved nature of the postparacrista and premetacrista. However, all crests on the molars of *Si. maddocki* are more weakly developed than in *Si. newtonae*, while the majority of crests are more weakly developed in *Si. gilli*. The postprotocrista, which is divided into two components, and the better developed upper molar midline crest of *Si. gilli* are the two exceptions. *Si. maddocki* may also be distinguished from *Si. newtonae* by the many very fine enamel crenulations that coat its loph surfaces. Overall, the molars of *Si. newtonae* are most similar to *S. andersoni*, but they differ by having the preparacrista much more strongly connected to the paracone apex, a stronger premetacrista, a stronger postmetaconulecrista and no continuation of the precingulum beyond the preprotocrista. Although a precingulum that does not extend lingually beyond the preprotocrista on the upper molars is unique to *Si. newtonae*, this condition is observed on the dP^3 of *S. andersoni*.

Dentary.

Si. newtonae is most similar in dentary size and morphology to *Si. brownei*, but the digastric eminence of the latter species is usually larger, as is the gradient of decreasing dentary depth anteriorly. In addition, the masseteric fossa is longer in *Si. brownei*, and the anterior root of the ascending ramus lies opposite the M_3–M_4 boundary or M_4 protolophid. In contrast, the anterior root in *Si. newtonae* leaves the ramus adjacent or just posterior to the M_4 hypolophid. The slightly procumbent diastema of *Si. newtonae* is not observed in any other *Simosthenurus* species, but is observed in *Sthenurus*, in *S. tindalei* Tedford 1966 and *S. stirlingi* Wells and Tedford 1995. The slender symphysis of *Si. newtonae* is most similar in size and form to that of *Si. brownei*, but it does not extend under the genial pit to the same degree, and its dorsal surface is nearly horizontal rather than anterodorsally-oriented. The narrow and deep median dorsal groove present in *Si. newtonae* is also characteristic of *Si. maddocki*.

Viewed posteriorly, the pterygoid fossa of *Si. newtonae* is narrower than in any other *Simosthenurus* species. Marked development of the processes overhanging the mylohyoid groove is similar to *Si. oreas* De Vis 1895, but the groove in the latter species is deeper and narrower.

Lower Dentition.

In size and morphology, the I_1 of *Si. newtonae* is intermediate in morphology between *Si. occidentalis* and *S. andersoni*. In this sense, the tooth resembles the I_1 of *Si. pales* De Vis 1895, but is much smaller. Size and general outline of the dP_2 is similar to *Si. occidentalis*, but the tooth is relatively narrower anteriorly. The shortness of the buccal crest is similar to that observed in *Si. maddocki*, but the dP_2 of this species is narrower and the main crest cuspules are more distinct. As with the P^3, the anterior width of P_3 is not markedly exceeded by the posterior width of the tooth. Overall, *Si. newtonae* is particular similar to *Si. brachyselenis* Prideaux and Wells 1997 in size and general morphology, but differs by being longer relative to the molars and having a slightly longer buccal crest. While the P_3 of the *Si. newtonae* holotype is similar in outline to that of *Si. brachyselenis*, other specimens of *Si. newtonae* often narrow more gradually anteriorly. Compared with '*Simosthenurus*' *cegsai* Pledge 1992, the *Si. newtonae* P_3 is more inflated posterobuccally, the median valley is usually wider, and the buccal crest is longer.

Although the protolophid base of the *Si. newtonae* dP_3 is narrower than the hypolophid base, the unworn crest of the protolophid is much narrower, similar to that of *Si. pales*. *Si. newtonae* appears to retain a paraconid lingual to the paracristid in the anterolingual corner of the dP_3 trigonid. A similar cusp is often observed on the dP_3 of other sthenurines, such as *Si. gilli*, *S. atlas* (Owen 1838) and *Hadronomas puckridgi*. Aside primarily from the stronger connection between the cristid obliqua and hypoconid apex, morphology of the *Si. newtonae* dP_3 is very similar to the succeeding molars. Among the species of *Simosthenurus*, the morphology of the *Si. newtonae* lower molars is quite unique. In some respects, their form more closely resembles species of *Sthenurus*, most especially *S. andersoni*. Similarities include the paucity of enamel crenulations on the lophid faces, the proximity of the paracristid and cristid obliqua to the buccal cusp apices, and the anterior turn of the lophid ends. Within *Simosthenurus*, the *Si. newtonae* lower molars most resemble *Si. gilli* in crown height and paucity of enamel crenulations, but are easily distinguished by their larger size, markedly inflated posterior face of the hypolophid, more curved transverse portion of the paracristid, and thicker, more buccally situated paracristid and cristid obliqua. A curved transverse portion of the paracristid is also observed in *Si. euryskaphus* Prideaux and Wells 1997 and many specimens of *Si. occidentalis*, but the paracristid and cristid obliqua of these two species are shifted more lingually, the lophid faces bear distinct fine enamel crenulations, and the lophid ends are less markedly turned anteriorly. In this latter feature and in the marked posterior inflation of the hypolophid, *Si. newtonae* is easily distinguished from all other *Simosthenurus* species.

Geographic Distribution

Simosthenurus newtonae is one of the most widely distributed Pleistocene sthenurine species. Overall, its distribution pattern most closely resembles that of *Si. occidentalis* (Fig. 1). Both species occur in late Pleistocene cave deposits in southwestern Australia (Merrilees 1979; Gully 1997), and were probably distributed across the southern periphery of the continent during periods when woodland or forest was more extensive. However, of these two species, only *Si. newtonae* has so far been recorded from Balladonia (= *Sthenurus atlas* in Glauert 1912) and the Nullarbor Plain (Lundelius, 1963; Lundelius and Turnbull 1989; Prideaux 1994; Aplin *et al.* 1995). Conversely, only *Si. occidentalis* is known from the Eyre Peninsula.

Remains of *Si. newtonae* and *Si. occidentalis* are commonly encountered in the cave faunas of southeastern South Australia (eg., Pledge, 1980; Wells *et al.*, 1984), although the latter species is much better known in Victoria. Together, they represent the only sthenurines known from late Pleistocene cave deposits in Tasmania, where *Si. occidentalis* is again by far the more abundant (Murray and Goede 1977; Goede and Murray 1979). While *Si. newtonae* is also known from southeastern Queensland (= *S. andersoni* in Bartholomai 1963), its only other occurrence north of the Monaro region in southeastern New South Wales is in the form of a large-toothed variant in the Kandos and Wellington Caves deposits.

Acknowledgments

The work presented here formed part of a Ph.D. degree undertaken at the Flinders University of South Australia on the systematics and evolution of sthenurine kangaroos. For discussions and advice I offer my sincerest thanks to Rod Wells, Dick Tedford, Peter Murray, Jim McNamara and David Ride. A great many of the specimens listed or described herein exist only because of the efforts of countless Flinders University students and volunteers who have assisted with the excavations in Victoria Fossil Cave over many years. Peter Daenke and Ed Bailey are commended for their excellent preparation of much of this material. I am indebted to Neville Pledge (South Australian Museum), Alisanne Ramsden (Queen Victoria Museum), Bob Jones (Australian Museum), John Long (Western Australian Museum), Ralph Molnar and Joanne Wilkinson (Queensland Museum), and Tom Rich and Betty Thompson (Museum of Victoria) for extended loans of fossil material. Bernie Cooke and Dick Tedford kindly reviewed the original manuscript and provided a number of constructive comments.

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